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Fluctuations in Populations of Collembola Within Leaf Litter in the Patuxent Research Refuge, Maryland

A DISSERTATION

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BY

John L. Ostdiek, O.F.M., M.S.

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Table of Contents

Introduction 1

Study areas 3

Methods and procedures 5

Observations 7

- Weather 7
- Collembola 8
  - Total number per dm^2 9
  - Total number per kgm dry wt. 11
  - Important genera 13
    - a. Hypogastrura 13
    - b. Onychiurus 15
    - c. Folsomia 16
    - d. Isotoma 18
    - e. Pseudosinella 19
    - f. Other genera 21
- Other faunal groups 22

Discussion 24

- Habitat 25
- Moisture 27
- Temperature 30
- Faunal relationships 31

Summary 33

Literature cited 35

Tables 41

Figures 45

Introduction

A growing bibliography, as seen in such publications as that of Salmon (1951, 1956), attests to an increasing awareness of the Order Collembola. Linnaniemi in 1907 published the first comprehensive work on the ecology of the springtails. Others followed, for example, Agrell (1941) and Strenzke (1949), who described the ecology of Collembola in various geographical areas. Many of these workers, such as Pearse (1946) and Bellinger (1954), reported on studies of populations. Although population studies are more numerous than other ecological studies, there is still great need for even more of them because of the large number of species in the order, in excess of 2,000, and the great abundance of individuals in practically all soils where vegetation grows (Murphy, 1955). Collembola are especially interesting because the curves based on sampling data are true population growth curves, reaching their maxima by the reproductive efforts of many rapidly breeding generations (Ford, 1937). The purpose of this paper is to describe fluctuations in populations of Collembola in four representative types of communities in eastern Maryland, U.S.A.: upland forest, bottomland forest, pine grove and grassland.

Study Areas

All collections were taken from four distinct communities on the Patuxent Research Refuge, Laurel, Maryland. The Refuge was particularly suitable because of its proximity to The Catholic University of America and its undisturbed areas. The 2,463-acre Refuge is located about 15 miles northeast of Washington, D.C. Geologically, it lies within the Fall-line Clay Hills District of the Atlantic Costal Plain Province. Physiographically, the area comprises three principal types: flood plain, terrace and uplands (Stickel, 1950). Hotchkiss and Stewart (1947) described the vegetation and classified it into communities. A map of the vegetational types of the Refuge, published by the Soil Conservation Service in 1945, indicates the location of plots within the blocks into which the Refuge has been divided and marked. Reference is made to this map in giving the locations of the stations.

Four stations, one in each community, were chosen for this study. The bottomland, an alluvial floodplain forest, comprises about 470 acres paralleling the Patuxent River. Numerous channels afford rapid drainage after floods and heavy rainfall. The station chosen was located just northeast of Duval Bridge in Plot 30 of Block 55. *Liriodendron tulipifera* L., *Betula nigra* L., *Nyssa sylvatica* Marsh., *Carpinus caroliniana* Walt., *Rhus radicans* L., *Podophyllum peltatum* L. and *Pteridium aquilinum* (L.) Kuhn were characteristic plants of the luxuriant vegetation. Despite heavy deposition of plant debris in such a forest, the Aoo (fresh litter) and Ao (partly decayed litter) horizons (U. S. Dept. Agric., 1951) particularly the latter, were poorly developed because of the frequent floods and alluviation. These horizons were hardly 5 mm thick.

The upland forest station was located on a slope in Plot 97-98 of Block 25. It is a comparatively young upland forest in which *Fagus grandifolia* Ehrh. and *Quercus alba* L. dominate, although some old *Pinus rigida* Mill.

and *Acer rubrum* L. could also be found. *Cornus florida* L. was frequent in the understory. The Aoo and Ao horizons were well-developed, measuring 2 to 4 cm in thickness. Roots were very abundant in the Ao layer. Often, a sharp line could not be detected between the Ao and A_1 layers.

The pine station was located in an isolated, old pine grove of about five acres in Plot 68 of Block 44. It was surrounded by cultivated fields and bordered by invading deciduous trees and shrubs. But at the site of the study area, the tree story consisted only of *Pinus virginiana* Mill. and *Pinus rigida* Mill. The duff, consisting of pine debris, was 1 to 4 cm in thickness. A rather sharp line separated the Ao from the A_1 layer.

The grassland was located on high upland to the north of the main laboratory buildings in Plot 33 of Block 26. In previous years this site, an old orchard, had been mowed. During the course of the study, though, no disturbance took place. *Festuca elatior* L. was very abundant, together with fairly abundant *Poa pretensis* L. Other plants noted were: *Rumex acetosella* L., *Oxalis stricta* L., *Allium vineale* L., *Rubus flagellaris* Willd., *Asclepias syriaca* L., *Oenothora sp.*, *Scirpus sp.*, *Ornithogalum umbellatum* L., *Holcus lanatus* L., and *Solanum carolinese* L. Very little plant debris had accumulated on the ground in this grassland. Some moss was present and this was collected in the samples together with the grass fragments.

Methods and Procedures

Biweekly field collections were begun in May, 1957 and terminated in September, 1958. Except on a few occasions, paired samples were taken from each station on each collection date, for a total of 236 lots. Paired samples, the first of which was random, were always taken within a few inches of each other (Macfadyen, 1952; Kevan, 1959) to minimize variation due to distance and to serve as a check or "control" one on the other. Within each habitat all samples were taken from a plot approximately 10 m^2, again to lessen variability ascribable to distance. Each station was carefully chosen as representative of the habitat.

Area, rather than volume, seems to be a more suitable basis for expressing population density (Macfadyen, 1952), so the following procedure was used. A sample was taken by laying a dm^2 quadrat on the forest floor, cutting down through the litter and humus with a sharp knife and removing the Aoo and Ao horizons. Most authors agree that the greater part of the soil fauna lives in these layers in the forest (Macfadyen, 1952). Thus the volume and weight of the samples varied, but the area and layers were constant.

The time of day at which the samples were collected varied somewhat from late morning to early afternoon. This, presumably, did not introduce a serious source of error, since daily migrations of Collembola seem to be chiefly conditioned by the degree of change in the relative humidity of the litter layers (Jacot, 1940).

The material was transported in soil cans to the laboratory, where, within two hours of collection, the extraction process was begun. A battery of modified Berlese funnels was used (most American authors continue to speak of them as Berlese, whereas Europeans prefer the name Tullgren). These were constructed of

8-inch metal funnels with baskets of 0.25-inch mesh hardware screening, so fitted as to provide "Haarløv passages" (Haarløv, 1947). The light and heat source above each funnel was a 25-watt bulb in an 8-inch funnel shade. An extraction period of 48 to 60 hours proved long enough, since no specimens dropped from the funnel when material was subjected to longer extraction periods.

Specimens dropped out of the sample material into collecting bottles containing 75 per cent ethyl alcohol. At the end of the extraction period, the Collembola floating on the surface of the alcohol were forced into the fluid by a few drops of ether (Glance, 1956). The bottles were then stored for later microscopic examination. After the completion of the extraction, the litter and humus material were oven-dried at 100° C. for 48 to 72 hours to determine water content.

The specimen samples were examined under the binocular dissecting microscope (12.5x to 80x magnif.) and the Collembola sorted out with an Irwin loop (Pennak, 1953). Individuals of the various genera and species in each lot were separated into dram vials and preserved as museum specimens. Simultaneous count was made on a modified abacus. All Collembola were counted and identified at least to genus. Representative specimens of the various genera were cleared and mounted in Hoyer's solution (Glance, 1956) for detailed taxonomic study.

Observations

Weather

The precipitation during the time of the study was recorded daily at the Patuxent Research Refuge. All other weather data came from the Glen Dale Bell Station, about three miles away, since it was the nearest weather station providing long-term data (Weather Bureau, 1957-8). In general, the summer of 1957 was unusually dry and that of 1958 unusually wet. The intervening winter was colder and wetter than normal (Fig. 1).

The precipitation pattern was most interesting because of the influence on soil fauna. No measurable rain fell from April 23 until May 11, 1957, and after that only in small amounts until 2.40 inches fell on June 6. By the end of July, a 10-inch deficiency since January 1, 1957 was reported. The state of dryness was comparable to similar drought periods in 1924 and 1955. Precipitation during the autumn approached normal, with some snow recorded on November 23. A heavy, 9-inch snow fell on December 4. This and subsequent precipitation caused the Patuxent River to overflow its banks on January 26 for the first time since the heavy flooding of July, 1956. A heavy snowstorm with strong winds struck Maryland on February 15, 1958, leaving an accumulation of 15 to 16 inches of drifting snow on the Refuge. By February 25, the drifts began to settle and vestiges remained until late March. Precipitation during April was very high, with some snow on April 10. Precipitation during May was below normal, reached normal in June and doubled the normal fall in July. This last month was outstandingly humid and wet, with some heavy rains. A total of 4 inches fell in one 24-hour period, July 8-9. Rains during August and September fell frequently but in small amounts.

Mean monthly temperatures during the study approximated the longterm averages except during the winter (Fig. 1). At noon on May 10, 1957, a high of 87° F was recorded. During June, temperatures exceeding 90° F were recorded on 11 days. During July, record heat days occurred on the 25th, 26th, and 27th. On September 27, the first frost of the season, a light one, was noted on the first terrace above the bottomlands and in low spots. On October 12, there was white frost on uplands as well as bottomland terraces. Frosty nights followed, with a warming trend on October 21 and 22. By November 11, thin ice had formed on water impoundments and 17° F temperature was recorded, the coldest to date. In December, minimum temperatures of 10° and 11° F were recorded on the 6th and 12th, respectively. The first half of January, 1958 was cold, with minimum temperatures of less than 10° F on five days, with a low of 7° F on January 10 and 13. On the collection date of January 21, the pine duff was frozen to a depth of about 1 cm. The soil in the grassland, too, was frozen. The humus and soil of the bottomland and upland were not frozen. The humus and soil of the bottomland and upland were not frozen. February was an exceptionally cold month, expecially during the middle of the month. Minima of 3° F on the 11th, 8° F on the 14th, 2° F on the 17th and 9° F on the 18th were reached. On February 12, the only collection date of the month, frozen mineral soil was noted at all stations, except the upland. In the pine and upland the Aoo layer was not frozen, but the Ao layer was. The litter of the bottomland and the moss of the grassland were unfrozen. During March, temperatures, though generally low, were closer to normal. The first days of May were quite rainy and warm with a maximum temperature of 86° F on May 4. Hot, humid weather started in late June and continued through July. The frequent rains and cloudiness kept the temperature slightly below average.

The Collembola

The numbers of Collembola, taken both as an order (Table 1) and by genera, varied considerably from station to station and sample to sample. The patterns of fluctuations of population density, as seen in a time series array, were somewhat obscured by the range of variation between the numbers within the paired samples. In some instances this range was greater than that between samples from different dates. This made it advisable, for the sake of analysis, to group the samples by season, rather than by date of collection.

Total number of Collembola per dm^2

Although the chief purpose of the study was to investigate the population fluctuations with time, it seems worthwhile to indicate first some observations on the frequency distribution. Three simple measures of frequency distribution: mean, median and range indicated seemingly significant variations among the four stations sampled (Table 2). The significance of these differences was difficult to ascertain because the numbers of springtails in the samples from each habitat fell into no recognizable distribution curve when grouped according to magnitude. Furthermore, the dispersion changed from season to season. Seasonal fluctuation of frequency distribution, as expressed by the derived values of coefficient of variation (Guilford, 1956), are shown in Fig. 2. The high of 163 per cent for the bottomland in the first summer was due in great part to the wide range of 0 to 63 Collembola per dm^2 in the eight samples for that season. The upland showed the least variation, the bottomland the most. No similarity of general pattern among the curves could be seen.

The general pattern of seasonal fluctuation in terms of unit area is indicated in Fig. 3. The most Collembola were collected from the pine site. The upland, bottomland and grassland followed in descending order. The curve for the grassland is not given because it would lie just above the baseline and show very little change. Although the curves are quite separate, the range between samples on distinct collection dates occasionally overlapped. On June 18, July 15, August 29 and November 18, 1957 and on February 12, June 6 and throughout the summer of 1958, the high sample of the upland exceeded the low sample from the pine grove. At no time was the count of the bottomland or the grassland greater than that of the pine grove. Only one bottomland sample, May 29, 1957, contained more Collembola than did the upland forest sample for that date. On September 10 and 23, October 9, December 17, 1957 and March 4, 1958, the high sample from the grassland yielded more Collembola than the low sample from the bottomland.

The pattern of seasonal fluctuation varied from station to station (Fig. 3). In both the pine and the upland the springtail populations first fell off during the late spring, then increased through the late summer and early fall. Low points in both habitats occurred on July 15. The rates of increase were about the same but the levels differed. During the winter, this rate remained fairly constant in the upland, but climbed steeply in the pine grove. The peak for both was reached in the latter part of December. Both stations showed a decreasing trend in the spring. In the pine this decrease was steady and fairly rapid, whereas in the upland it was slow and erratic from date to date. The decrease continued in the pine during the early summer and then leveled out. Meanwhile, the population of the upland reversed the trend by an increase to just slightly above the winter average.

In the bottomland the pattern of fluctuation varied noticeably from that of the pine and upland. The number of springtails per unit area was greatest during the late spring and early summer of 1957. Another population peak was reached in the same period of 1958. At other times the population density fluctuated around a mean of approximately 10 Collembola per dm^2.

As to the fourth habitat, the grassland, valid generalizations concerning population fluctuations were difficult to make because of the scarcity of specimens, as indicated by the low mean of 3.3 per dm^2 (Table 2). Unfortunately, a grassland with well-developed upper soil horizons was not available. Relatively few Collembola were collected from the litter and moss layers above the mineral soil (Table 1), even though the quadrat area was doubled for each sample. Therefore, it was difficult to determine a population trend.

A visual check of the data indicated that there was only, at best, a slight correlation among population fluctuations of the four habitats. To check this, the chi-square (X^2) and the contingency coefficient (C) were computed (Bailey, 1959; Siegel, 1956). The total number of Collembola per dm^2 from the bottomland and upland forests and the pine grove were grouped by seasons in an r x c contingency array. A value of X^2-595.98 significantly exceeded the value of 20.09 for 8 degrees of freedom at the 1 per cent level of confidence. Thus the seasonal totals of Collembola from the three habitats differed significantly. The value of C=0.240 was derived ($C= \sqrt{\frac{X^2}{N + X^2}}$, where N=9,729). It indicated that there was no significant relationship among the seasonal totals of Collembola populations from the three habitats.

To test the data further, a 2 x c contingency table (Bailey, 1959) was set up using seasonal total from only the pine grove and the upland forest. The value of X^2= 260.688 significantly exceeded the value of 15.09 for 5 degrees of freedom at the 1 per cent level of confidence. The value of C=0.166 (where N=9,266) again indicated that there was no significant relationship among the seasonal totals of Collembola from the pine and upland.

Total number of Collembola per kgm dry wt.

Many workers (cf. Strenzke, 1949; Wies-Fogh, 1948) are agreed that an ideal basis for expressing population figures of soil animals would be the surface area of the pore spaces in the soil available to each animal. But since no method of measuring this has been devised, it cannot be employed in practical studies (Macfadyen, 1952). As indicated, the samples of this study were collected on the basis of area. But the data obtained were also used to compute expected populations per unit dry mass of litter and humus. To express populations in terms of wet weight would not be valid because, 1) the ratio of water to litter mass would change more rapidly than the population density of the Collembola, and 2) there would be a time lag in the response of the Collembola natality and growth rates to the precipitation. Instead, the data from the dm^2 samples were used to compute by proportion a set of scores in terms of oven-dried mass. A kilogram was chosen as the unit.

The dispersion of the springtails in the pine, upland and bottomland was such that no recognizable frequency distribution curve could be found. But some observations are possible. There was less of a spread between mean and median values when Collembola populations were computed by weight (Table 3) than by area. In all three stations the dispersion, as measured by range of numbers of Collembola in the samples, was greater than in terms of area.

In general, the pattern of seasonal fluctuation appeared to be similar to that of unit area (Fig. 4). The sequence of pine, upland, bottomland, and grassland still remained; although now there was more overlapping of sample numbers, with the result that both the upland and bottomland curves were at a higher level than they were in terms of area. The curve for the pine appeared very similar in shape and magnitude to that for area. The rate of increase from the summer to the fall of 1957 was greater and the level of the spring somewhat lower. The resulting curve was steeper.

Within each season the dispersion among the samples from each habitat was expressed as a coefficient of variation. The seasonal trends of sample variation are graphed in Fig. 5. When compared to Fig. 2 the general patterns of the curves for the bottomland and the upland are quite similar, but different for the pine. In this last station, a peak of variation occurred in winter when populations were computed by weight, and in spring when sampled by area. Nearly the same sample variation occurred during both summers in the pine and bottomland but not in the upland. The magnitude of change in variation from season to season was greater per kgm than per dm^2. Also, the relative position of the curves for the pine and upland was reversed with the exception of the winter peak for the pine.

Important genera

The mean number of genera per sample varied by habitat and by season (Fig. 6). As could be expected, the relatively sparse populations in the bottomland were divided among fewer genera then in the upland and pine. The highest number of genera per sample in the bottomland was 7, reached on July 1, 1957 and May 12, 1958. The highest number in the upland was 12 genera per sample, reached on two dates: November 18 and June 6. The highest number of genera in the pine was 13 which occurred once, on August 22, 1958. Of the genera that appeared during the course of the study, some appeared in greater numbers and with greater constancy. There have been chosen for special comment in the following sections. A checklist of the 62 species collected is given in Table 4.

a. Hypogastrura

Specimens of Hypogastrura were collected from all four habitats. This genus was most numerous in the pine with a mean of 100 per dm^2, 9 per sample in the upland and less than 1 per dm^2 in the bottomland and grassland. Hypogastrura appeared in 100 per cent of the pine grove samples, 83 per cent of those from the upland, 36 per cent of those from the bottomland and 22 per cent of those from the grassland. This genus ranked first, numerically, in the pine, fifth in the upland, and sixth in both the bottomland and grassland. But too few specimens were found in samples from the two latter stations to provide adequate scores for statistical analyses.

In the pine Hypogastrura decreased from 111 specimens per dm^2 on May 14, 1957 and 218 on May 29 to a low of 3 specimens in each of the samples collected on August 29. Then the population density increased over the course of the fall and winter to a peak of 544 and 414 specimens in the paired samples of March 4, 1958. During this period, the fastest rate of increase occurred in December, so that by December 31 the two samples had 305 and 221 hypogastrurids. During late January and early February there seemed to be a small drop, followed by a rise, thus bringing into relief two winter peaks. During the spring of 1958, the density gradually declined from a high of 464 and 116 in the samples of April 10, to a low of 16 and 12 in those of June 6. Then in the summer there was a leveling out at approximately the same population density as during the previous summer.

In the upland, the numbers of Hypogastrura fluctuated around a mean of 7 individuals per dm^2 until December. Two winter peaks, corresponding to those in the pine were noted. The magnitude of these peaks, however, was far less, with 20 and 14 specimens found in the samples of December 31, and 17 in each of the samples of March 4. During the spring the populations decreased, but not in the gradual, steady decline found in the pine. In the summer a relatively high population density was reached, quite unlike the trend in the pine grove.

The general pattern of fluctuation of Hypogastrura (Fig. 7) is similar to that of the total number of Collembola per dm^2. The importance of this genus is brought out by the percentage of the total number of springtails made up of individuals of this genus (Fig. 8). The seasonal trends for the pine in both cases were remarkably alike, as were those for the upland, with the exception of the summer of 1957.

The variation of Hypogastrura between samples in each season seemed quite high (Fig. 9). Except for the autumn, variation in the pine paralleled that of the upland with the latter no longer consistently lower than the pine, as was the case in the general collembolan population. The relatively high coefficient of variation of 114 per cent for the pine and 117 per cent for the upland in the spring seemed to be due to a very significant decrease in population density during the course of the season.

When computed on the basis of dry weight of litter, the pattern of population fluctuation seemed to be the same as for area (Fig. 10).

b. Onychiurus

Onychiurus was next most numerous in occurrence. It was found in all four habitats with mean numbers per dm^2 of 29 in the pine, 19 in the upland, 4 in the bottomland and less than 1 in the grassland. Specimens of this genus were found in all the samples from the upland, 93 per cent of those from the pine. 82 per cent of those from the bottomland and 15 per cent of those from the grassland. Numerically, Onychiurus ranked first in the bottomland, second in both the pine and the upland, and seventh in the grassland. The upland samples, though, contained a higher percentage of Onychiurus than the pine. (Fig. 11).

The pattern of fluctuations of onychiurid populations in the pine and upland are shown in Fig. 12. Again, the grassland population was too small and irregular to give a true picture under the conditions of this study. The peaks of population density varied considerably in the other three stations. In the upland, there was a general winter high with maxima on December 31 (51 and 18 specimens) and March 4 (44 and 42 specimens). A summer peak was reached on August 22 when the paired samples contained 70 and 40 individuals. The trend in the pine was different. Two winter peaks on December 31 (14 and 143 specimens) and March 4 (67 and 10 specimens) were noted, too. But increase continued in the pine until April 10, when the paired samples contained 160 and 56 specimens. A steady decrease took place during the rest of the spring to a low of 4 specimens in each sample on June 6. From then on, the population fluctuated around a mean of 7 per dm^2 for the rest of the study. In the bottomland, there seemed to be an increase in density to a plateau during December followed by a drop during the late winter. In the spring and summer the general trend was one of increase, but far more variation between samples occurred here than in the other stations. Both the maximum and the minimum were reached in the paired samples for September 19, which contained 22 and 0 specimens.

The range of variation of samples between the pine and upland seemed significant (Fig. 13). The seasonal trends in the two stations paralleled each other except for the summer of 1958. The difference between the two summers in each station was reversed from the population per dm^2 (Fig. 12).

In terms of dry weight, a departure from the area picture was noted. The curves for the upland appear nearly alike in both instances, but those for the pine differ (Fig. 14). A mean of 769 per kgm over the course of the study for the upland just exceeded the mean of 733 for the pine. In the pine, an increase in the fall culminated in a peak of 2,872 and 1,299 on November 18. The high number of Onychiurus for the entire study, 5,053 per kgm, occurred in one of the samples of December 31. As noted above, there was also a steady drop in population density per kgm during the spring, from 2,941 and 1,069 on April 10, to 83 and 78 specimens on June 6. On those same dates the upland samples contained 255, 564 and 438, 1,514 Onychiurus, respectively.

c. Folsomia

Folsomia appeared at all seasons in the bottomland, upland and pine; but none were found in samples from the grassland. Over the course of the study, Folsomia averaged 22 individuals in the pine, 19 in the upland and 2 in the bottomland per dm^2. It was the first ranking genus, numerically, in the upland, third in the bottomland and fourth in the pine. Folsomia seemed to cluster more than the other numerous genera; since, 1) 45 per cent of the samples from the bottomland, 20 per cent from the pine and 3 per cent from the upland contained no Folsomia, and 2) there was wide variation among the samples (Fig. 14). This latter was especially the case in samples from the pine grove. The peak of this variation was reached on December 31, when one sample contained 285 Folsomia and the other 1. The highest variation between samples from the upland was on September 19, 1958, when the two samples contained 42 and 8 specimens. Too few Folsomia were found in samples from the bottomland for a justifiable analysis of variability.

The seasonal trends of population density per dm^2 can be considered in detail only for the pine and the upland (Fig. 16). In the upland the late summer (1957) was below average. Then in the fall, peaks occurred on September 23 (37 and 14 specimens in the paired samples) and November 18 (48 and 35 specimens in the samples). In the winter, the trend seemed to be one of decrease, although it was obscured by wide sample variation. From a low of 9 and 3 specimens in the samples of April 10, there was an increase to the high for the upland on May 12 of 47 Folsomia in each sample. The trend os slight decrease in the second summer again was obscured by wide sample variation.

In the pine, the Folsomia population density followed a different pattern. Both the summer and fall were significantly low, with Folsomia appearing in only 50 per cent of the summer samples. In the winter, there was only one large sample, that of December 31 with 285 individuals. This particular sample contained 85 specimens of Folsomia silvestrii, a species that normally appeared sparsely. During the rest of the winter and early spring the population density was quite low. By May 12, there was an increase (33 of 15 specimens in the samples) that led to a doubtful peak on June 6 of 60 and 5 individuals in the paired samples. In the summer, another doubtful peak was reached on August 22, when the samples contained 79 and 19 Folsomia.

The seasonal trend of percentage of Folsomia per sample in the upland (Fig. 17) was very similar to the fluctuations per dm^2 (Fig. 16) and per kgm (Fig. 18). The curve for the percentage in the pine was quite different from the dm^2 and kgm curves. Folsomia consistently made up less of the collembolan population in the pine than in the upland, except during the second summer.

The population density of Folsomia on the basis of dry weight followed seasonal trends that were similar to those for area (Fig. 18). A difference was that the spring peak for the upland was relatively higher than it was for area. An interesting note is that 10,071 Folsomia were computed for a pine sample of December 31, the highest number per kgm of any genus during the entire study.

d. Isotoma

Isotoma specimens were collected from all four stations at all seasons except during spring in the grassland. A mean of 21 individuals per dm^2 were found in the pine, 11 in the upland, 1 in the bottomland and less than 1 in the grassland. Isotoma ranked fourth, numerically, in the upland and pine, fifth in the bottomland and grassland. Specimens of this genus occurred in 93 per cent of the samples from the pine, 77 per cent of those from the upland, 38 per cent of those from the bottomland and 18 per cent of those from the grassland. In general, there seemed to be considerable clustering, as indicated by a fairly wide variation among samples (Fig. 19).

Only the pine and the upland populations were large enough for comparison and analysis (Fig. 20). In the summer of 1957, populations were low. No Isotoma appeared in the samples from the upland until August 29, and in the pine only about half the samples contained some. In the July 1 sample from the pine 41 specimens surprisingly appeared. No real peak in either habitat occurred until December 31, when the pine samples contained 17 and 90 specimens. The population then dropped below average during the rest of the winter, but increased in density during April to reach the high Isotoma peak for the study on May 12, when the samples contained 115 and 62 individuals. The late winter and spring increases were absent in the upland, but a peak was reached there in the summer on August 22, with 29 and 40 specimens in the samples. It is interesting to note how closely variation among samples agreed in the upland and pine. The general trend was one of decrease in sample variation (Fig. 19) and increase in population density (Fig. 20 and 21) and percentage of Isotoma per sample (Fig. 22).

The population density per kgm followed the pattern of fluctuation per dm^2. The only significant difference was the increased spread between the means for the pine and upland populations of the second summer (Fig. 21). The range for this season was 244 to 1,214 in the pine and 241 and 1,460 specimens per kgm in the upland. The highest number of Isotoma during the course of the study was one of 3,180 for a sample of December 31 from the pine.

e. Pseudosinella

Pseudosinella was the most numerous of the Entomobryidae. Individuals of this genus were collected in all seasons from the four stations, except during the spring from the grassland. Pseudosinella ranked second, numerically, in the bottomland, third in the upland and grassland, and fifth in the pine. Individuals occurred in almost all the samples from the upland and the pine, in 62 per cent of those from the bottomland and in 37 per cent of those from the grassland. A mean of 19 specimens per dm^2 appeared in the pine, 16 in the upland, 3 in the bottomland and less than one in the grassland. Sample variation of the pine was quite different from that of the upland (Fig. 23).

In general, the population density (Fig. 24) and the percentage of Pseudosinella per sample (Fig. 25) decreased over the course of the study in the three habitats analyzed. The pine showed the steepest population decrease. On August 15, 1957, a peak of 41 specimens per dm^2 occurred there, followed by another on September 23 of doubtful validity (96 and 6 specimens in the paired samples). A drop followed to a mean of 8 per dm^2 during the winter. Then during April and May, the population density rose to the overall average. No summer sample contained more than 5 specimens.

Less fluctuation occurred in the upland. The summer peak was reached before that for the pine, on August 1, when 37 specimens per dm^2 were collected. During the fall, contrary to the pine, no definite peak was evident, although there seemed to be a slight but steady decrease throughout the season. By the end of December, the population began to increase and reached a high for the upland on February 12, with 50 and 11 specimens in the paired samples. In the spring, the trend leveled out and then dropped fairly steadily during the summer to a low of 6 and 0 specimens in the paired samples of September 19.

The numbers appearing in the samples of the bottomland were all small, i.e. less than 10 per dm^2, with one exception: 54 specimens in the single sample collected on July 1, 1957. Because of such small scores, it was difficult to distinguish between sample variation and population fluctuation. But increases in density seemed to occur on February 12 (10 and 2 specimens in the samples) corresponding to the upland, and on May 12 (9 and 5 specimens). The rise in population density during the spring of 1958 (Fig. 24) is partly a reflection of the fact that Pseudosinella individuals were found in all but two samples, the highest percentage of occurrence for the bottomland, while the number per sample was not notably higher.

The seasonal trend of Pseudosinella per kgm followed the same general pattern as for area in the upland and pine, with some variation (Fig. 26). The population density was greater in the upland than in the pine, except during the fall. In the upland, peaks were reached on July 1, 1957 (1,463 specimens), February 12 (1,736 and 539 specimens) and May 12 (1,411 and 727 specimens), 1958. In the pine, peaks occurred on different dates, sc.: August 29 (377 and 1,549 specimens), September 23 (2,065 and 189 specimens) and October 9 (298 and 1,241 specimens), 1957.

f. Other genera

Among the other 27 genera collected, several should receive brief attention. Two Entomobryidae, Entomobrya and Tomocerus occurred frequently, but not in sufficient numbers to treat the population fluctuations statistically.

Entomobrya was most numerous during the late summer and early fall. In the pine, sufficient numbers were collected to give credence to a statement on population peaks. Population density increased in the summer of 1957 to a high of 33 and 80 specimens in the paired samples of August 29, 47 and 73 in those of September 23, and then decreased to an average of 1 per dm^2 through the winter and spring. During the second summer the Entomobrya populations increased only slightly. The seasonal trend was very similar to that of Pseudosinella. This same pattern seemed to hold for the bottomland and upland. Entomobrya appeared in 80 per cent of the samples from the pine, in 70 per cent of those from the upland, in 27 per cent of those from the bottomland and 10 per cent of those from the grassland. Six species of Entomobrya were collected, the most from any one genus. Using some of the specimens, Christiansen (1959) was able to put E. duolineata Bueker in synonymy with E. ligata Folsom.

Specimens of Tomocerus were collected at all seasons from all habitats except the grassland, where it was found only in the summer. Individuals appeared in 83 per cent of the samples from the pine, 60 per cent from the upland, and 58 per cent from the bottomland. The number in a sample was less than 10 except on three occasions: October 9, 1957 (12 specimens) and May 12, 1958 (12 specimens) in the pine and December 31 (11 specimens) in the upland. Hence, population fluctuations were difficult to distinguish from sample variation. But an increase in population density seemed to occur during the autumn in the pine and upland.

Several other Collembola were particularly noteworthy. Harlomillsia oculata appeared sporadically in samples from the pine. Only a few specimens were usually found in any one sample. But from the paired samples of September 10, 1957, 73 and 38 individuals were recovered. This indicates that unusual clustering and behavior could occur with regard to this epigeal oncopodurid. Orchesella was found chiefly in the pine and upland. Only on two occasions did more than 10 specimens appear in a sample. In general, few were found in the summer and fall of 1957. Thereafter, more appeared. Specimens of Orchesella were identified in 73 per cent of the samples from the pine grove, in 43 per cent of those from the upland, in 3 samples from the grassland and in 1 from the bottomland.

Other faunal groups

As is well known, many other groups of soil fauna are also extracted by the Berlese funnel technique. In this study, large numbers of Acarina were collected, together with lesser numbers of Insecta (both larvae and adult), Protura, Chilopoda, Diplopoda, Symphyla and Pseudoscorpionida. No attempt was made to count these non-collembolan groups, except the pseudoscorpions. These are well-known predators of Collembola (Cloudsley-Thompson, 1958) which would have a direct influence on the populations of springtails. Pseudoscorpions were collected from all four habitats and in all seasons. In the bottomland and grassland they averaged less than 1 per dm^2, 1 per sample in the pine and 3 in the upland. Specimens appeared in 75 per cent of the samples from the upland, in 47 per cent of those from the pine, in 19 per cent of those from the bottomland and in 11 per cent of those from the grassland. The highest numbers per sample appeared in the upland. One sample from July 9, 1958, contained 10 pseudoscorpions; another from August 1, 1957, contained 9. In general, these predators seemed to be most numerous during the warm months.

Discussion

The main objective of population ecology is to understand the processes responsible for fluctuations and trends of populations living in natural habitats. Owing to the inherent complexity of these processes, this objective is far easier to state than to fulfill (Neyman, Park and Scott 1958). Many factors are responsible for fluctuations within populations in the field. An investigator can only hope to sort through a small number of interactions of these factors and suggest which seem best to account for the population trends observed. Fortunately, some information on what environmental factors are most important to Collembola has been published. Weis-Fogh (1948) stated that in spite of the small amount of numerical material, it can be established that the successive changes in water content, variations in vegetation and the ecological factors connected with these, are accompanied by successive changes in the specific composition of the fauna.

One of the most difficult things to determine about any animal population is its size in nature (Slobodkin, 1958). This is especially true of soil-dwelling arthropods such as Collembola, becaus [illegible] our visual observation, necessitating, therefore, some sort of sampling technique. Very little information is available on the spatial size of Collembola populations. Glasgow (1939) found that four species of Onychiuridae occurred in definite colonies. Onychiurus armatus was aggregated into colonies about 3 inches in diameter; Onychiurus ambulans, Tullbergia quadrispina and T. krausbaueri in colonies at least 12 inches in diameter. We do not know how readily or how much the space occupied by a collembolan species population changes in response to enviromental variation. Very scarce also, is information on the distance between colonies of the same species.

These factors should be considered in the choice of the size of a quadrat, since the question of distribution is basic to the use of valid quantitative methods (King, 1939). But since information was so meager, the choice of the size for a quadrat in this study was influenced more by usage and suggestions of investigators. Baweja (1937) for example, recommended a plot size of 3 x 4 in. Bellinger (1954) used a circular quadrat about 64 sq. in. in area. Pearse (1946) used a still larger area, 1 sq. ft. A large size did not seem to be needed to sample colonies which were likely to occupy less area than the quadrat. The dm^2 quadrat size was chosen also because the extraction of organisms by Berlese funnel is less efficient when large amounts of material are in the funnel. There remains the possibility, though, that such a sample size was inadequate for at least some species, a fact that must be considered in evaluating the data obtained.

Students of soil arthropods warn that the Berlese funnel, even as modified by Tullgren (1918), Haarløv (1947), and Macfadyen (1953) and others, is a somewhat inefficient tool for quantitative studies. But it seems to be the best existing technique. Most Collembola respond to dessication of the soil atmosphere by moving horizontally and/or vertically. Only those that actually do so in the funnel will drop into the collecting bottle. The operation of the Berlese funnel was standardized as much as possible in this study, but nevertheless the data must not be accepted too precisely.

Habitat

The general collembolan population as well as some of the genus-population varied significantly from habitat to habitat. Pearse (1946), however, found no significant differences between populations in oak and pine woods on clay and sand, although particular species were more abundant in one or the other habitat. Gisin (1947) and Macfadyen (1952), on the other hand, concluded that given adequate analyses, there is considerable measure of correspondence of fauna with floristic groupings. Macfadyen also stated that macroscopic vegetation has a great influence on the density, but little effect on the species composition of the soil fauna. It seems that this influence would be mostly indirect, rather than direct, i.e. the macroscopic vegetation influences the microflora and microhabitat factors which help determine the collembolan populations.

Among various differences between a pine and a deciduous tree stand, an important one for soil fauna would be the litter. The autumnal fall of great amounts of leaves in the deciduous forest, besides adding the year's new material, also provides an insulating layer that prevents excessive change of temperature and drying within the lower layers. This would tend to protect those Collembola which need a high relative humidity. Also, the composition of the pine duff varies chemically and physically from that of the deciduous forest. During the warm months the pine duff is more likely to dry out between rains because of its lower water-holding capacity.

The soil atmosphere would, therefore, be less favorable for Collembola and for growth of fungi, their food. This seems to have been a contributing factor to the low population densities of the general collembolan population as well as the Hypogastrura and Onychiurus populations in the pine during the wet summer of 1958. The populations of these same groups were relatively dense in the upland. It should be added at this point, that those low populations might have resulted, in part, from a depletion of the food supply by the high winter and spring populations. During the winter there was an average of about 1.0 Hypogastrura together with 0.1 Onychiurus per cc of humus, a rather high density.

A special habitat factor, restricted in this study to the bottomland forest station, must be considered because of its influence on soil fauna. It is that of flooding. The bottomland was flooded twice during the course of the project. Neither flood caused any appreciable deposit of silt or removal of litter. But since the humus layer is almost non-existent, despite luxuriant vegetation, past floods have been severe. Such a shallow litter-humus layer cannot provide suitable conditions for large collembolan populations. First, the litter would dry out too much for Collembola that would not ordinarily descend into the mineral soil. The severity of the drying in the summer months must be lessened, to a certain extent, by a dense ground cover, principally of poison ivy, on a comparatively wet terrain. Secondly, there would be little protection from the low air temperature of winter, for those Collembola that are cold-sensitive.

The influence of the two floods on the Collembola populations was difficult to determine. No winter population peaks were noted in the bottomland, contrary to the pine and upland. The January flood could have been a contributing factor to this. The July flood seemed to cause a temporary decrease in population density, but recovery was rapid. The first samples taken shortly after both floods had receded contained Collembola, including late instars.

The general impression gained by a comparison of the four habitats was that the upland represented more of a steady-state in regard to the collembolan populations. Even though the pine duff often contained a denser population, it is, nevertheless, also true that there were fewer extremes of variation in the upland. No one genus dominated the collembolan fauna of the upland as seriously as Hypogastrura did in the pine, with the result that other genera there did not use a favorable period, such as the wet summer of 1958.

Moisture

The activity and abundance of Collembola are closely associated with the moisture content of the environment (Davidson, 1932). This is especially true of the Arthropleona, which lack tracheae, because cutaneous respiration can only be effective in animals living in a moist environment (Edney, 1957). The soil atmosphere is maintained in a moist condition by precipitation that is sufficient in amount and frequency. Precipitation provides soil water, which largely controls the other aspects of the soil environment (Collis-George, 1959), especially the relative humidity of the soil atmosphere.

Because of anatomical features, not all species of Collembola depend equally upon high relative humidity in their environment. The tracheae of the Symphypleona free species of this suborder from much of the restrictiveness of cutaneous respiration. This explains, to some extent at least, why sminthurids were proportionately more abundant in the bottomland and grassland. In those habitats, the thin litter layers were subjected to frequent periods of evaporation. The vestiture of long hairs and scale of Entomobryidae fit them, too, for life in a less humid atmosphere than is possible to Collembola lacking these structures. This seems to explain why, in the face of reduced competition during the summer of 1957, significantly high populations of Pseudosinella and Entomobrya appeared in the pine, upland and bottomland stations. Hypogastrura, Onychiurus, Folsomia and Isotoma lack those protective structures, and hence, their populations were low during the dry summer, apparently because they lacked protection from drying out.

One of the first expected responses to changes in the relative humidity of the microhabitat of Collembola would be for them to move away from unsuitable conditions. Evidence for such movement is given in the clearest possible fashion by the process by which the Berlese funnel operates (Bellinger, 1954). The movement, as Pearse observed (1946), is to deeper layers, since there is a wide variation of moisture conditions in the upper two inches of the forest floor because of crown density, openness of stand, and distribution of rainfall through the year (Jacot, 1940). How many Onychiurus, Folsomia and Isotoma reacted to the lack of moisture in the summer of 1957 by migrating to the A_1 layer, is impossible to say on the basis of this study.

Such movement is often temporary and does not affect the actual numbers in the populations. But wide changes in the relative humidity do directly influence the population number by affecting such phenomena as the rates of natality, mortality and development. Davis and Harris (1936) demonstrated that eggs of *Pseudosinella petterseni* (=*violenta*) ceased to be viable when subjected to relative humidity less than 50 per cent for five days. Davidson (1932) observed that eggs of *Sminthurus viridis* remain dormant in the soil during the South Australian dry season. This condition was not because of a definite rhythmical diapause, but was enforced by lack of moisture. The eggs could be induced to hatch with suitable moisture and temperature. Ripper (1930) found that *Hypogastrura manubrialis* could survive at humidities of 50-60 per cent, but needed an atmosphere at or near saturation for development. Strebel (1932) reported that *Hypogastrura purpurascens* died after one day's exposure to a relative humidity of 55 per cent. The population increases of *Onychiurus*, *Folsomia*, *Isotoma* and *Hypogastrura* in the litter and humus layers during the fall of 1957 indicated an increased natality and/or a re-invasion of those layers in response to better moisture conditions brought about by increased precipitation and lower temperatures.

A lack of moisture may also indirectly limit collembolan populations. One such way would be by limiting the food supply. A brief survey of the work on the food of Collembola inhabiting the soil suggests that the most important substances are fungi, decaying plant remains and detritus (Poole 1959). Schaller (1949) examined collembolan gut contents and found that fungal hyphae were the predominate constituent. Fungal cells were observed, too, in the guts of many specimens during the course of this study. The soil, and particularly the humus layer, supports a large and varied flora of small fungi (Bellinger, 1954). These fungi need moist conditions in which to grow. Low precipitation would diminish or even stop growth. Collembola, usually active animals, would then be driven to find a new food supply or eventually starve. In both cases, a reduced population of springtails in the litter would result. Presumably, this was one of the phenomena occurring in the summer of 1957, that would help explain the significantly low populations.

Temperature

The Collembola are considerably less influenced by the temperature than the moisture, but higher temperatures, particularly if the rise is rapid, are not favorable to them. Their tolerance of frost is, however, high (Kuhnelt, 1955). Volz (1934) is satisfied that frost causes no marked changes in the vertical distribution, although there seems to be vertical migration of a few inches (2 to 4 inches) with certain species, notably such as Onychiurus spp. (Jacot, 1940). The high populations of Onychiurus found in the upland and pine during the winter do not agree with Jacot's statement. Bellinger (1954) found in samples taken from a mixed stand of white pines and hemlocks in Connecticut, that the major portion of soil fauna was in the part of the humus layer which was frozen solid.

Temperature seems to affect especially the development of Collembola. The duration of the instars depends greatly on temperature. The length of instars of Tomocerus vulgaris is almost doubled when the temperature is lowered 10° C within the range of 12°-22° C (Agrell, 1948). This, if generally true of other species, could help explain the proportionately high number of early instars observed during the winter. Folsom (1916) observed that in Massachusetts, Hypogastrura armata overwintered in the egg stage. Wray (1945) reported a unique occurrence of this species in mid-February in North Carolina, which seems to indicate the springtails wintered in an active stage. At the Patuxent Refuge, large numbers of Hypogastrura were found during winter, even in frozen samples. The difference in climate between Maryland and Massachusetts seems to be sufficient, therefore, to bring about this variation in life cycle.

Faunal relationships

Population fluctuations reflect, also, the influence of competition and predation. These two, of course, are not the only biotic factors at work in a faunistic group such as the soil fauna, but they are singled out here for special comment.

Competition may be of two kinds, intraspecific and interspecific. In regard to Collembola, very little data has been published on the subject. Davis and Harris (1936) observed that individual Pseudosinella petterseni (=violenta) would not stay in contact with one another. If one would get too close to another the antennae were used to strike the intruder away. This behavior seems to indicate an intraspecific competition. Whether or not such behavior is common to other genera and species is not known. If it is the case, in varying degree at least, it would help explain some of the observed densities. For example, the Hypogastrura, it would seem, can tolerate close physical proximity of their own kind, because of the actual, high density found.

Agrell (1941) concluded that competition between individual Collembola does not seem to assert itself noticeably until the springtail population rises to about 500-600 animals per 400 cc. Samples taken from the pine during the winter and early spring approached or exceeded this "threshold". Perhaps such numbers depleted the food supply so severely that a population decrease, if not a crash, followed despite the favorable climatic conditions of the wet summer. Judging from such evidence as that of Baweja (1939), it seems that Hypogastruridae are more agressive, since they increased 18.5 times and 21.8 times in sterilized field plots, whereas the Onychiuridae failed to regain their normal numbers and Entomobryidae and Isotomidae showed an increase of only 1.5 - 2.2 times over the control plot.

A second faunal relationship of great importance in population ecology is that of predation. A number of animals are known to prey upon Collembola. Agrell (1941) inferred that gamasid mites are predators. Cloudsley-Thompson (1958) stated that pseudoscorpions feed on Collembola. Pseudoscorpions were the only known predators that were counted in this study. Since there were so few in the pine, especially during the winter, it is quite conceivable that the mortality rate of springtails was thus lowered enough to enable them to reach dense populations. The relative abundance and constancy of the pseudoscorpions in the upland, on the other hand, seemed to be a contributing factor to the relative steady-state of the Collembola populations there.

Summary

1. This paper reports on the population fluctuations of Collembola in four representative types of habitats of Maryland: upland forest, bottomland forest, pine grove and a grassland. All stations were located on the Patuxent Research Refuge, near Laurel, Maryland.

2. Biweekly samples were begun in May 1957 and terminated in September, 1958. Paired samples, each a dm^2, were taken from the Aoo and Ao horizons. The Collembola were extracted by a modified Berlese funnel technique.

3. The summer of 1957 was unusually dry and that of 1958 unusually wet. The intervening winter was colder and wetter than normal with above average snowfall. The bottomland station was flooded twice during this study in January and July, 1958.

4. The numbers of Collembola, taken collectively as an order or by genera, varied considerably from station to station and sample to sample. The largest numbers of Collembola as an order were collected from the pine The upland, bottomland and grassland followed in descending order.

5. The pattern of seasonal fluctuation varied from habitat to habitat. A winter peak of a mean of 426 Collembola per dm^2 occurred in the pine. A winter peak of 111 and a summer peak of 113 springtails in the upland and a spring maximum of 21 per dm^2 occurred in the bottomland. Valid generalizations concerning the grassland were difficult because of the sparseness of specimens

6. A total of 62 species in 32 genera were collected. The six species of Entomobrya collected, were the most for any one genus.

7. Hypogastrura, which ranked first in the pine, reached

a peak of 299 specimens per dm^2 in the pine during the winter, with a top number of 544 individuals in a sample collected on March 4, 1958. During the winter, this genus accounted for 70 per cent of the Collembola collected from the pine duff. The high numbers of this genus seemed to deplete the food or bring about other changes in the pine, so that populations of Collembola during the favorable summer of 1948 were quite low.

8. Onychiurus was second in numbers of individuals. Peaks of populations occurred on December 31 and March 4 in the upland, December 31 and April 10 in the pine. This genus ranked first in the bottomland, and second in the pine and upland.

9. Folsomia seemed to cluster more than the other numerous genera. There was wide variation among the samples. This genus ranked first in the upland, third in the bottomland, and fourth in the pine.

10. Isotoma ranked fourth in the pine and upland, fifth in bottomland and grassland. There seemed to be considerable clustering. But despite this, variation among samples from pine and upland agreed quite closely from season to season. The peak was reached in the pine on May 12.

11. Pseudosinella was the most numerous of the Entomobryidae. The populations of Pseudosinella and Entomobrya decreased, in general, over the sixteen-month period, possibly because of interspecific competition.

12. Pseudoscorpions were the only known predators of Collembola that were counted in this study. They were collected from all four habitats, but were most constant and numerous in the upland, appearing in 75 per cent of the samples from that station, with a mean of 3 specimens per dm^2. They seemed to be a contributing factor to the relative steady-state of Collembola populations there.

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Table 1. Total number of Collembola per dm^2 from May 14, 1957 to September 19, 1958. Paired samples are designated as A and B. Single samples were taken until August 15, 1957.

Season	Date	Bottomland		Upland		Pine		Grassland	
		A	B	A	B	A	B	A	B
Spring	May 14	4		101		213		8	
	May 29	18		13		529		6	
	June 18	20		171		110		1	
Summer	July 11	63		107		216		5	
	July 15	8		28		8		0	
	Aug. 1	0		65		65		0	
	Aug. 15	2		28		126		1	
	Aug. 29	6	18	35	63	58	248	2	0
	Sept. 10	1	0	21	110	305	205	2	4
Fall	Sept. 23	5	12	111	77	274	144	9	3
	Oct. 9	6	8	46	26	48	207	4	10
	Oct. 22	9	19	54	–	–	–	–	–
	Nov. 5	11	8	127	–	–	–	–	–
	Nov. 18	11	16	118	109	193	90	0	0
	Dec. 3	17	6	–	–	–	–	–	–
Winter	Dec. 17	4	8	69	163	630	735	3	4
	Dec. 31	21	10	188	95	349	748	2	4
	Jan. 21	4	4	–	–	–	–	–	–
	Feb. 12	19	6	129	27	94	279	3	3
	Mar. 4	17	6	128	99	646	441	4	8
Spring	Mar. 27	10	19	–	–	–	–	–	–
	Apr. 10	21	26	41	44	714	227	8	2
	Apr. 24	14	15	–	–	–	–	–	–
	May 12	39	35	130	110	332	270	3	5
	May 26	13	36	–	–	–	–	–	–
	June 6	15	12	91	160	126	50	1	1
Summer	June 24	33	–	–	–	–	–	–	–
	July 9	–	–	30	123	109	62	7	8
	July 25	9	6	–	–	–	–	–	–
	Aug. 8	1	9	–	–	–	–	–	–
	Aug. 22	7	19	175	152	172	68	1	1
	Sept. 5	25	12	–	–	–	–	–	–
	Sept. 19	35	5	80	117	117	53	0	1

Table 2. Means, medians and ranges of the total numbers of Collembola per dm^2 during the course of the study.

	Bottomland	Upland	Pine	Grassland
Mean	14.0	90.3	245.0	3.3
Median	11	95	205	3
Range	0-63	13-175	8-748	0-10

Table 3. Means, medians and ranges of the total numbers of Collembola per kgm dry weight of litter and humus during the course of the study. The grassland totals were too low to permit valid estimations of the numbers of Collembola per kgm.

	Bottomland	Upland	Pine Grove
Mean	1855	3723	5205
Median	1447	3443	4332
Range	0-13,125	818-8699	537-26,338

Table 4. Checklist of the species of Collembola identified in the samples taken from the Patuxent Research Refuge during the course of this study. The families are listed according to Gisin 1944. Taxonomic descriptions for each species as noted: [1] Mills, 1934; [2] Maynard, 1951; [3] Folsom, 1937; [4] Christiansen, 1958; [5] Bonet, 1944; [6] Guthrie, 1903; [7] Handschin, 1928; [8] Folsom, 1913; [9] Wray, 1948; [10] Denis, 1933; [11] Goto, 1953; and [12] Harvey, 1895.

Poduridae

- _Frisea_ _claviseta_ Axelson, 1900[1]
- _Hypogastrura_ _armata_ (Nicolet, 1841)[2]
- _Hypogastrura_ _humi_ (Folsom, 1916)[2]
- _Hypogastrura_ _macgillivrayi_ (Folsom, 1916)[2]

Micranurida pygmaea Börner, 1901[1]
Neanura barberi Handschin, 1928[2]
Odontella cornifer Mills, 1934[1]
Paranura sexpunctata var. *colorata* Mills, 1934[1]
Pseudachorutes saxatilis Macnamara, 1920[1]
Pseudachorutes subcrassoides Mills, 1934[1]
Xenylla grisea Axelson, 1900[1]

Onychiuridae
Onychiurus pseudarmatus Folsom, 1917[2]
Onychiurus ramosus Folsom, 1917[1]
Onychiurus subtenuis Folsom, 1917[1]
Tullbergia granulata Mills, 1934[1]

Isotomidae
Folsomia elongata (MacGillivray, 1896)[3]
Folsomia fimitaria (L.)[3]
Folsomia nivalis (Packard, 1873)[3]
Folsomia quadrioculata Folsom, 1937[3]
Folsomia silvestrii Folsom, 1937[3]
Folsomides parvus Folsom, 1937[3]
Folsomina onychiurina Denis, 1931[1]
Isotoma andrei Mills, 1934[1]
Isotoma minor Schäffer, 1896[3]
Isotoma trispinata MacGillivray, 1896[3]
Isotomodes tenuis Folsom, 1937[3]

Entomobryidae
Entomobrya assuta Folsom, 1924[4]
Entomobrya atrocincta Schott, 1896[4]
Entomobrya griseoolivata (Packard, 1873)[4]
Entomobrya ligata Folsom, 1924[4]
Entomobrya nivalis (L.)[4]
Entomobrya sinelloides Christiansen, 1958[4]
Entomobryoides mineola (Folsom, 1924)[4]
Harlomillsia oculata (Mills, 1937)[5]
Lepidocyrtus christianseni Goto, 1953[11]
Lepidocyrtus cyaneus Tullberg, 1871[1]
Lepidocyrtus cyaneus var. *cinereus* Folsom, 1924[1]

Orchesella ainsliei Folsom, 1924[1]
Orchesella hexfasciata (Harvey, 1895)[12]
Orchesella zebra Guthrie, 1903[6]
Pseudosinella candida Folsom, 1902[1]
Pseudosinella decemoculata (Guthrie, 1903)[2]
Pseudosinella duodecimocellata Handschin, 1928[7]
Pseudosinella petterseni Börner, 1901[2]
Salina decorata Mills, 1932[1]
Tomocerus bidentatus Folsom, 1913[8]
Tomocerus flavescens var. *americanus* Schott, 1896[8]
Tomocerus lamelliferus Mills, 1934[1]
Tomocerus vulgaris (Tullberg, 1871)[1]

Sminthuridae
Arrhopalites binoculatus (Börner, 1901)[1]
Deuterosminthurus macgillivrayi Banks, 1899[9]
Megalothorax tristani Denis, 1933[10]
Neelus minutus Folsom, 1901[2]
Neosminthurus curvisetis (Guthrie, 1903)[1]
Ptenothrix marmorata (Packard, 1873)[2]
Ptenothrix oswegatchiensis Maynard, 1951[2]
Sminthurides lepus Mills, 1934[1]
Sminthurinus aureus (Lubbock, 1862)[2]
Sminthurinus elegans (Fitch, 1863)[2]
Sminthurinus latimaculosus Maynard, 1951[2]
Sminthurinus similitortus Maynard, 1951[2]
Sminthurus fitchi Folsom, 1896[2]

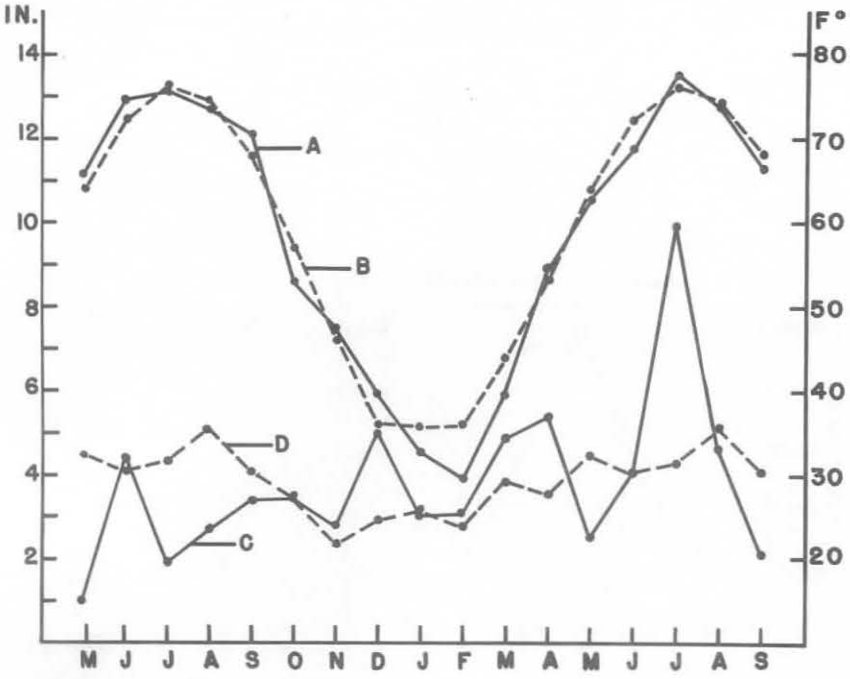

Fig. 1. Monthly meteorological data for the period of this study, beginning with May, 1957 (M) and ending with September, 1958 (S). Actual monthly mean temperatures (A) and long-term mean monthly temperatures (B) are given in °F. Actual total precipitation for each month (C) and long-term mean monthly total precipitation (D) are given in inches. Long-term means are based on a 25-year period.

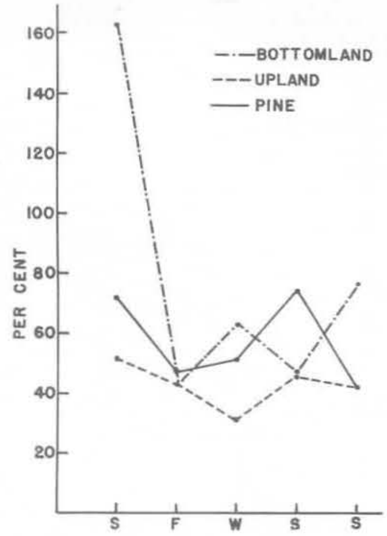

Fig. 2.

Coefficients of variation of numbers of Collembola per dm^2, expressed in percentage, by season from the summer of 1957 through the summer of 1958. In this and the following figures the first S signifies summer, F fall, W winter, S spring and the final S summer.

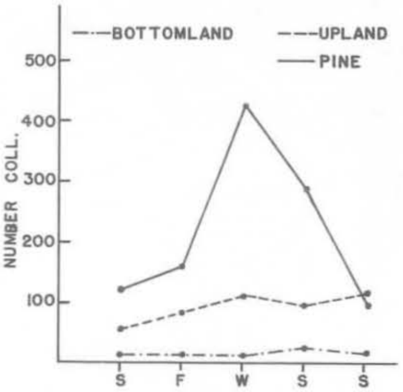

Fig. 3.

Mean numbers of all Collembola per dm^2 by season from the summer of 1957 through the summer of 1958.

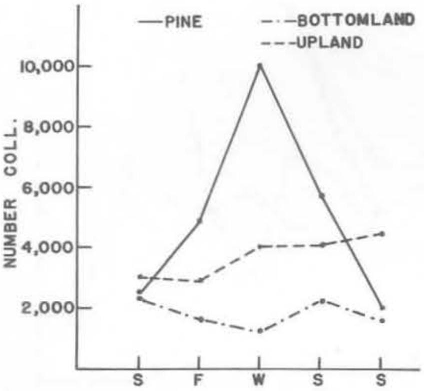

Fig. 4.

Mean numbers of all Collembola per kgm dry weight of litter and humus by season from the summer of 1957 through the summer of 1958.

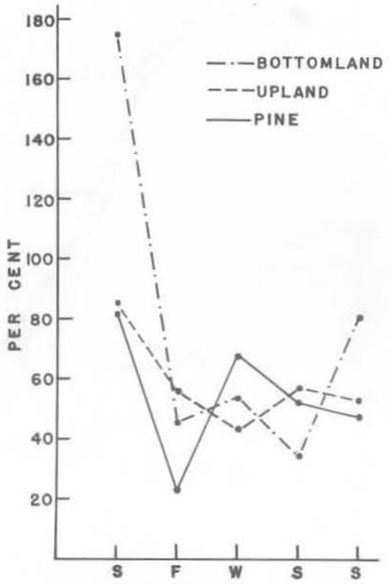

Fig. 5.

Coefficients of variation of numbers of all Collembola per kgm dry weight of litter and humus, expressed as per cent, by season from the summer of 1957 through the summer of 1958.

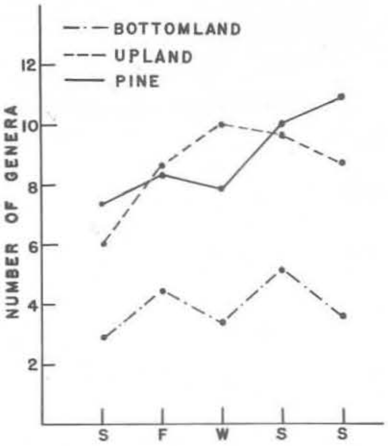

Fig. 6.

Mean numbers of genera per dm^2 sample by season from the summer of 1957 through the summer of 1958.

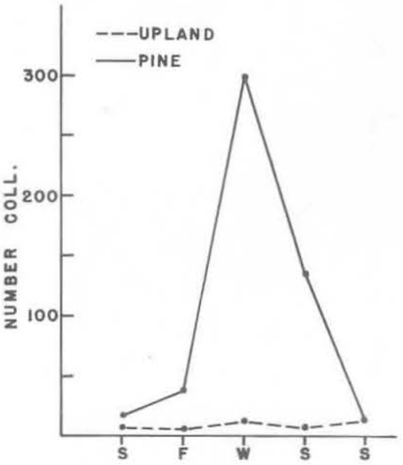

Fig. 7.

Mean numbers of Hypogastrura per dm^2 by season from the summer of 1957 through the summer of 1958.

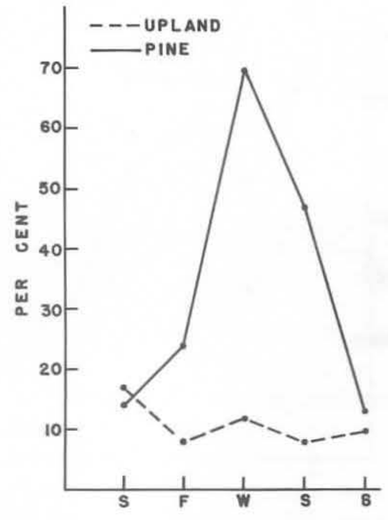

Fig. 8.

Mean percentage of Hypogastrura of the total number of Collembola per dm^2 by season from the summer of 1957 through the summer of 1958.

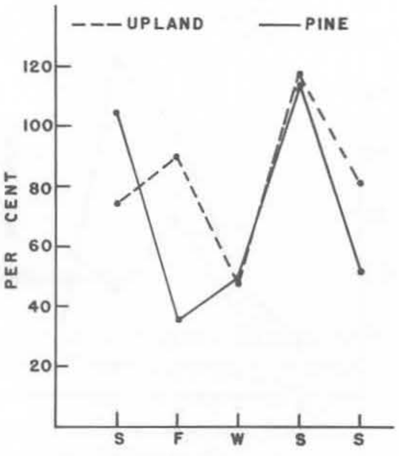

Fig. 9.

Coefficients of variation of numbers of Hypogastrura per dm^2, expressed in percentage, by season from the summer of 1957 through the summer of 1958.

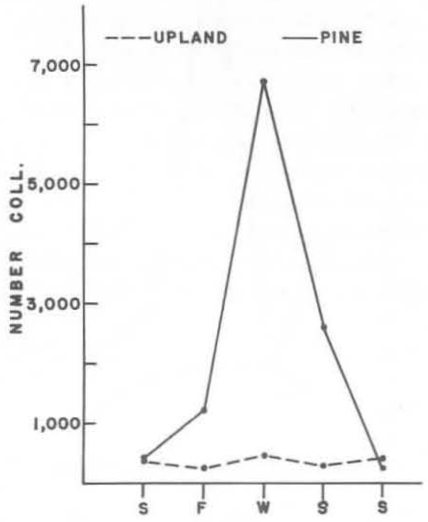

Fig. 10. Mean numbers of Hypogastrura per kgm dry weight of litter and humus by season from the summer of 1957 through the summer of 1958.

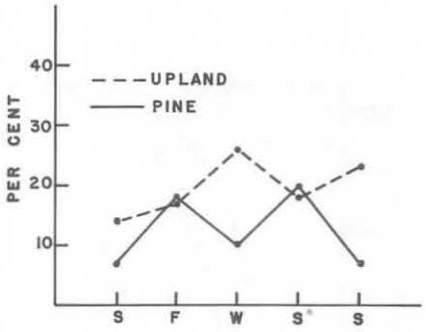

Fig. 11. Mean percentages of Onychiurus of the total number of Collembola per dm^2 by season from the summer of 1957 through the summer of 1958.

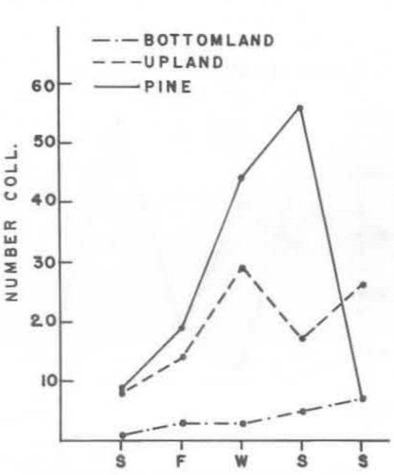

Fig. 12.

Mean numbers of Onychiurus per dm^2 by season from the summer of 1957 through the summer of 1958.

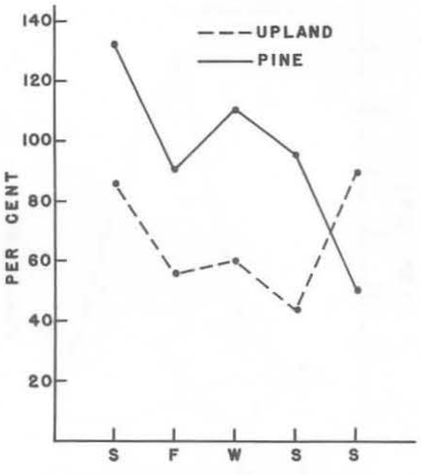

Fig. 13.

Coefficients of variation of numbers of Onychiurus per dm^2, expressed in percentage by season from the summer of 1957 through the summer of 1958.

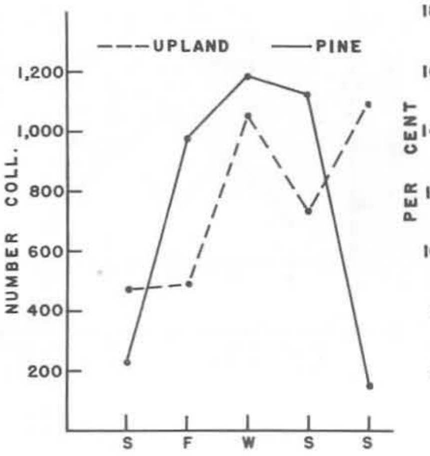

Fig. 14.

Mean numbers of Onychiurus per kgm dry weight of litter and humus by season from the summer of 1957 through the summer of 1958.

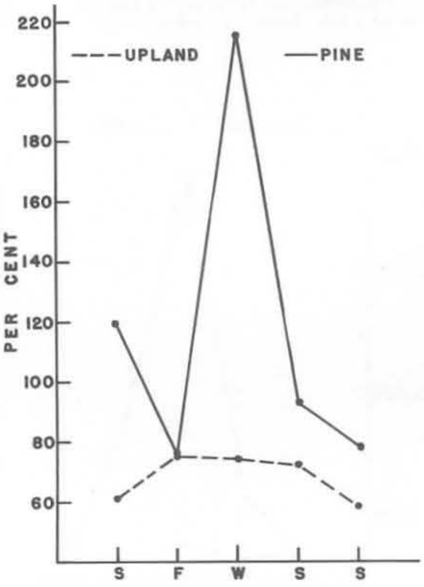

Fig. 15.

Coefficients of variation of numbers of Folsomia per dm^2, expressed in percentage, by season from the summer of 1957 through the summer of 1958.

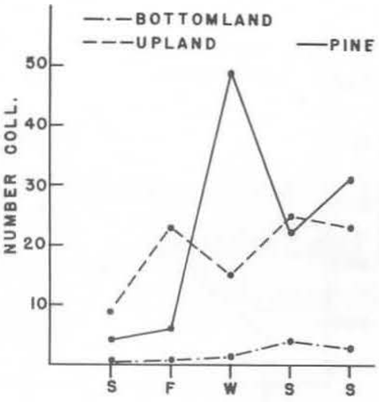

Fig. 16.

Mean numbers of Folsomia per dm^2 by season from the summer of 1957 through the summer of 1958.

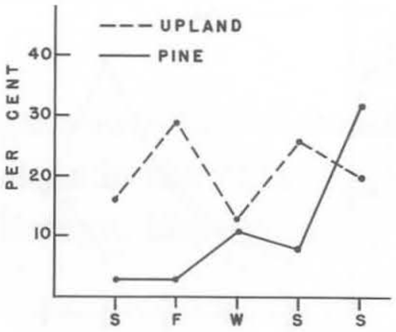

Fig. 17.

Mean percentages of Folsomia of the total number of Collembola per dm^2 by season from the summer of 1957 through the summer of 1958.

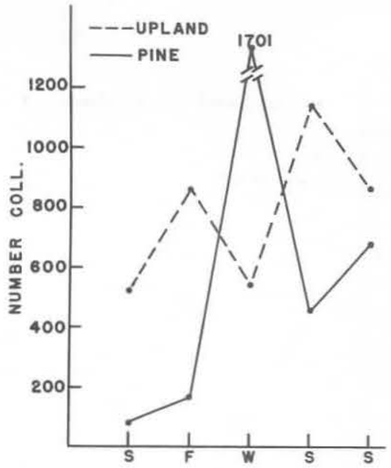

Fig. 18

Mean numbers of Folsomia per kgm dry weight of litter and humus by season from the summer of 1957 through the summer of 1958.

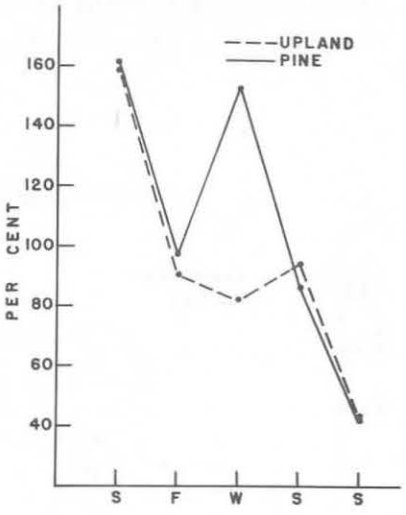

Fig. 19.

Coefficients of variation of numbers of Isotoma per dm^2, expressed in percentage, by season from the summer of 1957 through the summer of 1958.

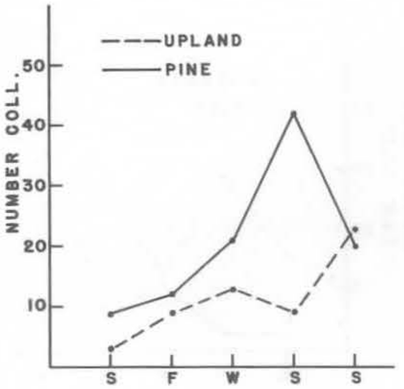

Fig. 20.

Mean numbers of Isotoma per dm^2 by season from the summer of 1957 through the summer of 1958.

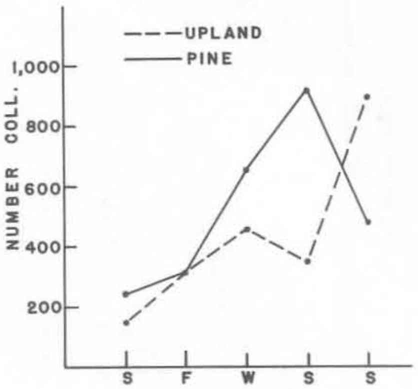

Fig. 21.

Mean numbers of Isotoma per kgm dry weight of litter and humus by season from the summer of 1957 through the summer of 1958.

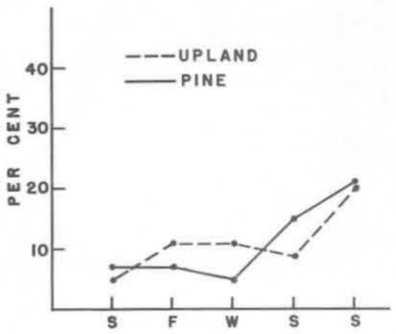

Fig. 22.

Mean percentages of Isotoma of the total number of Collembola per dm^2 by season from the summer of 1957 through the summer of 1958.

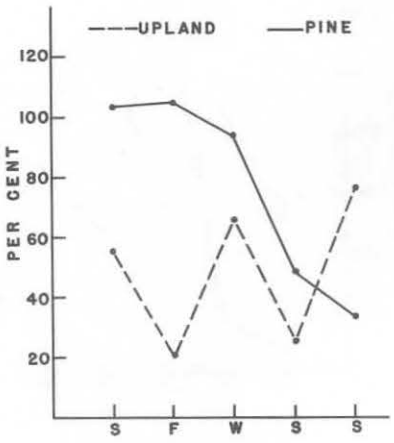

Fig. 23.

Coefficients of variation of numbers of Pseudosinella per dm^2, expressed in percentage, by season from the summer of 1957 through the summer of 1958.

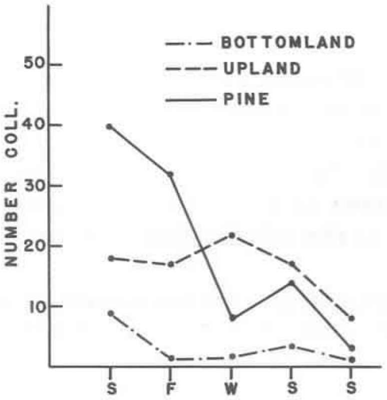

Fig. 24.

Mean numbers of Pseudosinella per dm^2 by season from the summer of 1957 through the summer of 1958.

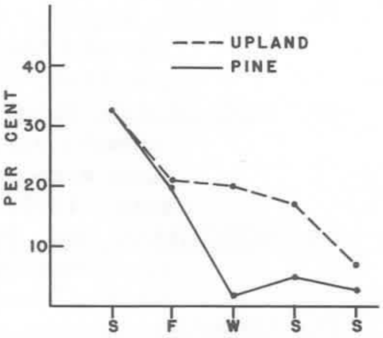

Fig. 25.

Mean percentages of Pseudosinella of the total number of Collembola per dm^2 by season from the summer of 1957 through the summer of 1958.

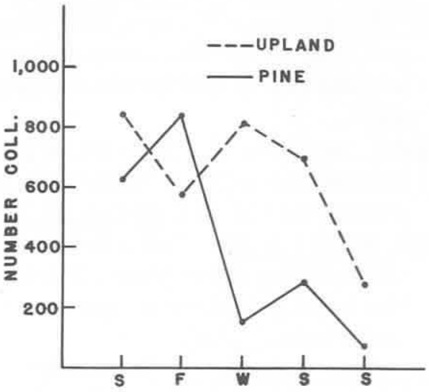

Fig. 26.

Mean numbers of Pseudosinella per kgm dry weight of litter and humus by season from the summer of 1957 through the summer of 1958.